Vulnerability of Subarctic and Arctic breeding birds

Anouschka R. Hof,1,2,5 Genoveva Rodríguez-Castañeda,3 Andrew M. Allen,4 Roland Jansson,1 and Christer Nilsson1

1Landscape Ecology Group, Department of Ecology and Environmental Science, Umeå University, Umeå SE-901 87 Sweden
2Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin 53706 USA
3Section of Integrative Biology, University of Texas in Austin, 205 W. 24th Street, Austin, Texas 78712 USA
4Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences (SLU), Umeå SE-901 83 Sweden

Abstract. Recent research predicts that future climate change will result in substantial biodiversity loss associated with loss of habitat for species. However, the magnitude of the anticipated biodiversity impacts are less well known. Studies of species vulnerability to climate change through species distribution models are often limited to assessing the extent of species’ exposure to the consequences of climate change to their local environment, neglecting species sensitivity to global change. The likelihood that species or populations will decline or go extinct due to climate change also depends on the general sensitivity and adaptive capacity of species. Hence, analyses should also obtain more accurate assessments of their vulnerability. We addressed this by constructing a vulnerability matrix for 180 bird species currently breeding in Subarctic and Arctic Europe that integrates a climatic exposure-based vulnerability index and a natural-history trait-based vulnerability index. Species that may need extra conservation attention based on our matrix include the Great Snipe (Gallinago media), the Rough-legged Buzzard (Buteo lagopus), the Red-throated Pipit (Anthus cervinus), the Common Swift (Apus apus), the Horned Lark (Eremophila alpestris), and the Bar-tailed Godwit (Limosa lapponica). Our vulnerability matrix stresses the importance of looking beyond exposure to climate change when species conservation is the aim. For the species that scored high in our matrix the future in the region looks grim and targeted conservation actions, incorporating macroecological and global perspectives, may be needed to alleviate severe population declines. We further demonstrate that climate change is predicted to significantly reduce the current breeding range of species adapted to cold climates in Subarctic and Arctic Europe. The number of incubation days and whether the species was a habitat specialist or not were also among the variables most strongly related to predicted contraction or expansion of species’ breeding ranges. This approach may aid the identification of vulnerable bird species worldwide.

Key words: Arctic region; biodiversity; birds; climate change; natural history traits; specialists; species distribution modeling; Subarctic region.

Introduction

Ongoing and future climate change will have profound effects on species richness and species’ geographic distributions, threatening many species with extinction (Sala et al. 2000, Thomas et al. 2004, Urban 2015). In general, climates are shifting poleward or becoming nonanalogous compared to previous conditions (Williams et al. 2007), forcing species to adapt to new climates or track their current climatic niches in order to survive (Parmesan et al. 1999, Walther et al. 2002, Meltofte 2013). Species inhabiting high-latitude regions are thought to be particularly sensitive to climate change, since they have adapted to climates that will no longer exist, or will be severely reduced (ACIA 2005). Also, variability in population abundances has shown to be larger at higher latitudes, which means that these populations may be more at risk from extinctions than populations at lower latitudes (Oliver et al. 2014). Changes in species interactions and food availability associated with climate change may have greater impact than direct effects of climate change like increased temperatures and UV-B radiation (Cahill et al. 2013). Large numbers of species’ distributions are shifting poleward (Auer and King 2014, Gillings et al. 2015), and many Arctic species are less likely to cope with the increased competition, predation and diseases that these new species bring (Callaghan et al. 2004).

The vulnerability of species to climate change, i.e., the likelihood that species or populations will decline and eventually go extinct due to climate change, does not depend solely on their exposure to the consequences of climate change to their local environment. (Williams et al. 2008, Dawson et al. 2011). The sensitivity and adaptive capacity of species to climate change should also be determined to obtain more accurate vulnerability assessments. Nevertheless, most studies apply species distribution modeling (SDM) to predict the impact of future climate change on species’ geographic distributions using
only climatic variables (Pearson and Dawson 2003, Guisan and Thuiller 2005, Rodríguez-Castañeda et al. 2012). Most studies disregard the potential effect of species interactions, as well as anthropogenic and other abiotic factors, although there is an increasing appeal from the research community to include such factors (Dawson et al. 2011, Bellard et al. 2012). A few studies have demonstrated the potential, and importance, of incorporating species interactions in SDMs (Araújo and Luoto 2007, Hof et al. 2012a, Kissling et al. 2012, Hof 2015), but opportunities to introduce such factors are limited (Hof et al. 2012a). For example, incorporating the future food availability of a generalist species would be conceptually and computationally difficult.

There are also other approaches to increase the understanding of the possible impact of future climate change on species. One is to use information on the ecology of species to help determine which species produce reliable SDMs based on climate data only (McPherson and Jetz 2007, Hanspach et al. 2010). Another is to incorporate the physiology of species into SDMs to model the key fitness components of species. This allows for combinations of multiple fitness components to identify the niche of the organism (Kearney and Porter 2009). Other studies have combined SDMs based on climate data with information on the physiology (e.g., development temperature of butterflies; Buckley et al. 2011) and population dynamics (Swab et al. 2012) of species to improve predictions of for example climate change responses. Finally, since specific species traits, such as thermal tolerance, may enhance vulnerability to climate change (Deutsch et al. 2008), some studies have called for or already incorporated natural history traits of species in vulnerability assessments (Williams et al. 2008, Heikkinen et al. 2010, Foden et al. 2013, Garcia et al. 2014). Garcia et al. (2014) developed a novel framework for amphibians where the spatial overlap between (1) projections of climate change-induced threats and opportunities and (2) the occurrence of species that have traits, such as dispersal ability and sensitivity to climate, that potentially mediate species responses to climate change, were integrated to improve predictions of species responses. However, this framework is less suitable for species such as birds with high dispersal abilities and a wider range of thermal tolerances. For example, many bird species occur over a wide range of temperatures, migrating for instance between polar and tropical regions. Foden et al. (2013) assessed the global-scale vulnerability of birds to climate change by estimating their exposure to changes in sea level, temperature, and precipitation, and a limited number of traits such as their capacity to respond by dispersal or evolutionary change, and their sensitivity due to habitat specialism, environmental tolerance, dependence on interspecific interactions, and rarity. The work of Triviño et al. (2013) included a risk assessment of breeding birds in the Iberian Peninsula by combining the exposure to climate and land-use, their vulnerability to change based on seven traits and their current conservation status.

In this paper, we introduce a vulnerability matrix based on two separate indices so that the matrix incorporates both exposure to climate change and inherent vulnerability due to natural-history traits. This should aid the prioritization of species conservation, that is, help identifying species in need of extra attention to guide conservation and monitoring activities. Furthermore, if specific vulnerability traits are identified, targeted actions may be suggested to alleviate threats related to those vulnerability traits, thus enhancing species persistence. The exposure-based vulnerability index is created using traditional predictive models and the natural-history trait-based vulnerability index is based on twelve traits related to the adaptive capacity and sensitivity of species to climate change. In total, we investigated the vulnerability of 180 breeding bird species in Subarctic and Arctic Europe to climate change. By doing so we aim to increase the understanding of the potential impacts of climate change on Subarctic and Arctic breeding birds and aid the assessment of species vulnerability to a changing climate.

**Methods**

**The exposure index**

The climatic exposure index was based on the vulnerability of bird species’ geographic breeding ranges in the Subarctic and Arctic part of Norway, Sweden and Finland (i.e., Fennoscandia in Europe; Fig. 1) to climate change. Our study region was limited to this part due to limited availability of detailed species occurrence data for many other regions in the Subarctic and Arctic parts of the Western Palearctic. Since the aim of our study was to assess the likelihood that the extent of the climatically suitable area for breeding will increase or decrease in the study region, we used the extent of the regional rather than that of the global climatic breeding range. We used this approach because species may be differently classified on local and global red lists; a population may be locally but not globally endangered. For example, the White-backed Woodpecker (*Dendrocopos leucotos minor*) is assessed as critically endangered on the Swedish red list, as vulnerable on the Finnish red list (Tiainen et al. 2016), but as least concern on the Norwegian red list and on the global red list (BirdLife International 2014; Swedish and Norwegian red lists available online). Moreover, 98% of the species in our analyses are globally assessed as least concern on the IUCN Red List of Threatened Species, which should indicate that there are globally no large differences in their vulnerability at present (list available online). As a comparison, only 74% of the species in our analyses were assessed as least concern on the Swedish red list (also see Appendix S1: Table S1). Furthermore, it may be better to assess local

6 http://artfakta.artdatabanken.se/
7 http://data.artdatabanken.no/Rodliste
8 http://www.iucnredlist.org/
populations rather than global populations due to differences between populations in, for example, the type of habitat they utilize, their phenotype, and the different biotic pressures they face (Post et al. 2009). To assess the local vulnerability in our study region we therefore did not account for the global range.

We used the SDM algorithm MaxEnt (Phillips et al. 2006), which has shown to generally outperform other algorithms (Elith et al. 2006, Hijmans and Graham 2006), to predict the ranges that are and will be climatically suitable for breeding for the studied species. MaxEnt only needs presence records to generate predictions; absence records are taken randomly from the extent of the geographic region used to train the model (Phillips et al. 2006, Elith et al. 2011). However, different results may be obtained when using different geographical extents (Anderson and Raza 2010). Using a large extent, meaning that a large climatic variety is used to generate predictions, can lead to an overestimation of the area suitable for a species. On the other hand, when a small geographic extent is used, one risks that the full climatic niche of the species concerned is not captured, leading to underestimations (Thuiller et al. 2004). We set the extent of the geographic region used to train the model to include the study region and an additional zone of approximately 1,000 km south of the study region. It thus included the entirety of Norway, Sweden, Finland, and the Baltic States, since many species are expected to shift or expand their geographic ranges to higher latitudes (Parmesan et al. 1999, Walther et al. 2002, Huntley et al. 2008). In this way, we captured the full climatic variation that is predicted to occur in the study region in future.

We collected occurrence data for 251 bird species breeding in the Subarctic and Arctic part of Fennoscandia (Fig. 1). These data were obtained for the breeding season (June–August) for the period 2000–2009 from
nationalspeciesoccurrence databases (Artsobservasjonen, Artportalen, and Hattika), and from the data portal of the Global Biodiversity Information Facility (databases available online).\(^9\)\(^,\)\(^10\)\(^,\)\(^11\)\(^,\)\(^12\) Occurrences with a detail up to 1 km\(^2\) were included to match the scale of other data. Our data set included only those species for which we had ≥30 occurrence records after adjusting for spatial differences in sampling effort. Occurrence data sets are often biased due to differences in sampling effort; data for Sweden were for instance over-represented in comparison to data for the other countries. As a remedy, we randomly deleted excessive occurrences using a raster (grid size ~10 km\(^2\)), with the aim to have no more than one randomly chosen occurrence data point per 10 km\(^2\) grid-cell.

The climate projection for 2.070 used in this study was the downscaled general circulation HadGEM2-ES (Hadley Global Environment Model- Earth System) under the 4.5 Representative Concentration Pathway (RCP), available at WorldClim (available online).\(^13\) We chose this RCP since it is neither the mildest nor the most extreme scenario. Although the world is currently on track for the 8.5 scenario we wanted to be cautious and underestimate rather than overestimate vulnerability so that the most vulnerable species can be targeted for conservation. Our aim was further to see the direction of change; a more extreme warming scenario would likely lead to qualitatively similar results but would be more extreme. We used the commonly used 19 bioclimatic variables that were derived from monthly temperature and rainfall values during 1950–2000 as variables in the models (available at WorldClim),\(^14\) at the most detailed scale possible, 30 arc-seconds (~1 km\(^2\)), in order to capture environmental variability (Hijmans et al. 2005). In addition, landcover, available at the 30 arc-seconds scale from the Global Landcover Facility and human population density (obtained from the European Distributed Institute of Taxonomy), often used to represent anthropogenic impacts in predictive studies (Algar et al. 2009, Morueta-Holme et al. 2010), were included in the models as static variables (data available online).\(^15\)\(^,\)\(^16\) Furthermore, a number of species were associated with coastal environments. Distance to coast was therefore entered in the models as a static variable in order to avoid inland areas being predicted as suitable for coastal species. Some degree of spatial autocorrelation between bioclimatic variables is unfortunately unavoidable. Testing for spatial autocorrelation for presence-only data is not possible (Dormann et al. 2010) and since we judged all included variables to be potentially biologically meaningful, we did not pre-select variables. Instead we took advantage of the regularization application of MaxEnt, which deals with the selection of environmental variables (regulating some to zero). Regularization prevents MaxEnt from matching the input data too closely, which may lead to “overfitting” of the data, which has a negative effect on the predictive performance of models (Phillips and Dudik 2008). This application has shown to perform well and is thought to outperform pre-selecting procedures like PCA (Hastie et al. 2009, Elith et al. 2011). Since the model outcome can vary based upon the order with which variables are entered in the models, which is an automated process carried out by MaxEnt that randomizes the order of the variables, models were run 10 times for each species. These replicates were averaged in order to obtain an index of relative habitat suitability for the species assessed, based on recommendations by Marmion et al. (2009). We used the default convergence threshold (10\(^{-6}\)) and maximum number of iterations (500). Hinge features model more complex relationships in the training data and substantially improve model performance. They were therefore applied, as recommended by Phillips and Dudik (2008).

MaxEnt predicts the suitability of the region for species as a continuous variable. This was transformed into binary suitable/unsuitable area by applying the maximum training sensitivity plus specificity logistic threshold defined by MaxEnt as a cutoff. We chose this method since it has shown to be one of the superior methods to transform continuous probabilities of species occurrence to binary presence/absence occurrence (Liu et al. 2005). The extent of, and overlap between, the predicted current and potential future ranges were calculated. Species were assumed to be fully able to disperse, given that birds are highly mobile. We used the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Hanley and McNeil 1982, Phillips et al. 2006) to assess the accuracy of predictions of SDMs. In addition, we set aside a randomly obtained 30% of the occurrence data as testing data in order to compare the AUC of these models with that of the training models, which consisted of the remaining 70% of the occurrence data. Models for which the average AUC of the predictions were <0.75 did not perform sufficiently and have been excluded from the analyses. Analyses were therefore limited to 180 species.

To create the exposure index we formulated three criteria based on the outcomes of the SDMs to which we assigned scores of 2 (vulnerable), 1 (mildly vulnerable), or 0 (not vulnerable) (Table 1). For the first criterion, we determined the percentage of the study region that is currently climatically suitable during the breeding season, and classified these as either small (<5% of the study region), medium (5–20%), or large (>20%). For the second criterion, we used the same conditions to determine whether a species future breeding range in the study region is predicted to be small (<5%), medium (5–20%), or large (>20%). For the third criterion, we determined whether the proportion of stable area was

9 http://www.artobservasjonen.no
10 http://artportalen.se
11 http://www.hattika.fi
12 http://data.gbif.org
13 http://www.worldclim.org/cmip5_30s
14 http://worldclim.org/bioclim
15 http://www.landcover.org
16 http://edit.csic.es/HumanPopulation.html
Table 1. List of reviewed natural history traits for the traits index of bird species breeding in Subarctic and Arctic Europe and their range loss or gain as determined by the species distribution modeling for the exposure index and their corresponding vulnerability scores.

<table>
<thead>
<tr>
<th>Characteristic/trait</th>
<th>Possibilities</th>
<th>Score</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Exposure index</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Current size of the breeding range in the study region (% of the study region)</td>
<td>&lt;5%</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>5–20%</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>&gt;20%</td>
<td>0</td>
</tr>
<tr>
<td>Future size of the breeding range in the study region (% of the study region)</td>
<td>&lt;5%</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>5–20%</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>&gt;20%</td>
<td>0</td>
</tr>
<tr>
<td>Stable area: percentage of current breeding range that remains suitable in future</td>
<td>&lt;25%</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>25–50%</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>&gt;50%</td>
<td>0</td>
</tr>
<tr>
<td><strong>Traits index</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Migrating</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Long (sub-Saharan/to southeast Asia)</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Short</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Sedentary</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Diet breadth</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prefers to feed on a couple of items</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>No preferred food item</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Habitat specialist</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Largely dependent on a singular biome</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Not dependent on a singular biome</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Ground nesting</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yes</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>No</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Average clutch size (based on quartiles)</td>
<td>&lt;4 eggs</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>4–6 eggs</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>&gt;6 eggs</td>
<td>0</td>
</tr>
<tr>
<td>Number of incubation days (based on quartiles)</td>
<td>&gt;26 d</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>14–26 d</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>&lt;14 d</td>
<td>0</td>
</tr>
<tr>
<td>Number of fledging days (based on quartiles)</td>
<td>&gt;38 d</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>15–38 d</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>&lt;15 d</td>
<td>0</td>
</tr>
<tr>
<td>Length of the breeding season (based on quartiles)</td>
<td>&lt;2 months</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>2–3 months</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>&gt;3 months</td>
<td>0</td>
</tr>
<tr>
<td>Typical number of broods (based on quartiles)</td>
<td>1 brood</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>2 broods</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>&gt;2 broods</td>
<td>0</td>
</tr>
<tr>
<td>Adult survival rates (based on quartiles)</td>
<td>&lt;0.46</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>0.46–0.73</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>&gt;0.73</td>
<td>0</td>
</tr>
<tr>
<td>Age at first breeding (based on quartiles)</td>
<td>&gt;2 yr</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>2 yr</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>1 yr</td>
<td>0</td>
</tr>
<tr>
<td>Maximum lifespan (based on quartiles)</td>
<td>&lt;11 yr</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>11–23 yr</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>&gt;23 yr</td>
<td>0</td>
</tr>
</tbody>
</table>
small (<25%), medium (25–50%) or large (>50%). Stable area is the area that is predicted to be climatically suitable for the species to breed both currently and in future. For example, a species for which the current climatic range was predicted to be $1 \times 10^7$ km² and the future climatic range $1 \times 10^6$ km², of which $5 \times 10^5$ km² overlapped with the current climatic range and thus is stable, received for the first criterion a 1, since $1 \times 10^7$ km² is approximately 8% of the study region and that is >5% but <20%. For the second criterion it received a 2, since $1 \times 10^6$ km² is approximately 1% of the study region and that is <5%. For the third criterion it received another 2, since only $5 \times 10^5$ km² from the $1 \times 10^7$ km² of climatic range it originally had remains suitable, that is, is stable, which is 5%. We assumed that each criterion was equally important as the other criteria. We summed all scores and divided the sum by the maximum score possible (6) and thus created an index on a scale from 0 (not vulnerable) to 1 (very vulnerable). Using different thresholds for assigning scores would result in different outcomes; some species may fall in different categories when different thresholds would be used. However, regardless of threshold levels, our index provides guidance to which species are among the most or least vulnerable ones in our study region; the most vulnerable and the least vulnerable species would always end up in their respective categories irrespective of the threshold chosen.

The traits index

We used the AnAge database (Animal Ageing and Longevity Database), life history data published by Möller (2006), consulted websites from the British Trust for Ornithology, the Encyclopedia of Life, and the online bird guide Avibirds, and consulted the volumes of The Birds of the Western Palearctic by Cramp and Perrins (1994) to obtain information about a number of species traits which may potentially affect how species respond to climate change, making them more resistant or extra vulnerable (data and websites available online).17, 18, 19, 20 When more than one resource provided data for a species, we averaged the values or used the values from the resource that provided data on the most number of traits for that particular species. We collected information about whether the species is migrating or not, diet breadth, whether the species is a habitat specialist, that is, whether it is largely dependent on a singular biome, ground nesting, average clutch size, number of incubation days, number of fledging days, the length of the breeding season, typical number of broods, adult survival rates, juvenile survival rates, and age at first breeding. Unfortunately, data on the typical or average lifespan were only available for a limited number of species. We thus used the maximum lifespan, being aware of the limitations of using this parameter: measures of longevity may, for instance, depend on the intensity with which a species has been studied. Some traits, that is the number of incubation days, fledging days, survival rates, length of the breeding season and the number of broods, vary within species depending on latitudinal position. We, however, used the average or typical values available for each species, which reduces potential bias between species that, for example, produce multiple broods in temperate regions and species that do not.

Unfortunately we could not find information on several parameters for a number of species. We lacked data for the number of fledging days for 1% of the species, the maximum lifespan for 5%, the age at first breeding for 7%, adult survival rates for 12%, the length of the breeding season for 19%, and juvenile survival rates for 51% of the species. We therefore omitted the parameter “juvenile survival rates” but we used a regression tree based on parameters for which we had data for all species to estimate the lacking data for the other parameters (Burgette and Reiter 2010, Higashijima et al. 2010).

We included migration as a trait that may make species more vulnerable with climate change, since such species rely on multiple climatic niches during the year (Elphick 2007). One could argue that since climate change is expected to be more pronounced in high-latitude regions, species that do not migrate may be more vulnerable than those that migrate, since the latter “escape” to less affected regions. However, migrating species face additional threats. First, climate change can amplify temporal mismatches between migratory avian predators and their prey (Both et al. 2006). It is also thought that long-distance migrants become more vulnerable since they have to face a longer sequence of decisions preceding and determining the start of reproduction (Knudsen et al. 2011). We included diet breadth, and whether the species is a habitat specialist or not in our index since species that are dependent on specific prey items or specific biomes are more vulnerable than species that are not. For example, due to climate change the cycles of lemming (Lemmus spp.) populations have been altered (Kausrud et al. 2008), which in turn has affected reproductive success of the snowy owl (Bubo scandiacus) in Fennoscandia, since it specializes on this prey (Schmidt et al. 2012). We included ground nesting in the index since important consumers of eggs of ground-nesting birds and predators of their juveniles, like the American mink (Neovison vison) and the West-European hedgehog (Erinaceus europaeus), are predicted to expand their ranges northward in future (Hof et al. 2012b). Both these species have already shown the capacity to threaten populations of ground-nesting birds (Nordström et al. 2003, Jackson et al. 2004, Tjernberg 2010b). We included survival rates, lifespan, and natural history traits that are related to reproduction, such as average clutch size and the number of broods, in the index since the effect of a potential failure of a brood, or death of a juvenile, due to for instance extreme weather events that are thought to

17 http://genomics.senescence.info/species/
18 http://www.bto.org/about-birds/birdfacts
19 http://eol.org/
20 http://www.avibirds.com/
be increasingly common with climate change (Rajczak et al. 2013), is larger for species with lower reproductive capacity. We included the number of incubation days since species that need to spend a longer time incubating inevitably face potential threats over a longer period of time than those that need to spend shorter times incubating. We included length of the breeding season as this incorporated factors that were not related to the number of broods or number of incubation days. Birds with a long breeding season may have benefits related to greater flexibility in egg-laying dates, due to for example adverse weather conditions. Birds with longer breeding seasons may also initiate a second breeding attempt in the event of a failed brood.

The traits index was based on all of the above-mentioned natural history traits (Table 1). Again we assigned scores of 2 (vulnerable), 1 (mildly vulnerable), or 0 (not vulnerable) to the traits (Table 1). The thresholds between the scores (2, 1, 0) assigned are, when possible, based upon quartiles (Table 1), which is a conservative approach. We assessed the vulnerability of a large number of species, but data on the difference in vulnerability between, for example, species that lay two eggs vs. species that lay three or four eggs are largely unavailable. We therefore had to choose thresholds arbitrarily, which needs to be kept in mind while drawing conclusions from our study. In a few cases (e.g., ground nesting) we only had vulnerable and not vulnerable categories, which then received a 2 and a 0, respectively. The migratory status of a species had three classes: long (i.e., from Fennoscandia to sub-Saharan or to Southeast Asia) = 2, short (i.e., from Southern Europe) = 1, sedentary (at least part of the population overwinters in the region) = 0. Of course, one trait might weigh more heavily than another. However, it is difficult to ascertain how the weights should be distributed as this will vary among species. We therefore chose to weigh each factor equally, assuming that each trait is equally important in determining the vulnerability of the species. Furthermore, all traits have to be considered on an equal basis to be able to deem the vulnerability of the species groups identified. We summed all scores and divided the sum by the maximum score possible (24) and thus created an index on a scale from 0 (not vulnerable) to 1 (very vulnerable). The exposure index and the traits index were then combined in a matrix to aid the assessment of species’ vulnerability.

**Relating contraction or expansion to climatic variables and natural history traits**

In an attempt to relate the predicted future contraction or expansion of species’ breeding ranges in the study region to global rather than regional climatic variables and to natural history traits we used random forest analyses. Based on the results of the SDMs, we classified the species in two groups: those that were predicted to lose part of their breeding range in future due to climate change and those that were predicted to increase their current breeding range in future due to climate change. Random forest analysis combines decision trees which can be used to identify which variables are important in distinguishing between groups; in other words, random forest analysis tell us which climatic variables and natural history traits characterize expanders and which characterize contractors. We used the RandomForest package (Liaw and Wiener 2002) in R version 3.1.1 (R Core Team 2014), setting aside 20% of the species to test the accuracy of the prediction, to identify if and which species traits are related to contracting and expanding species’ breeding ranges.

In addition to the natural history traits mentioned in the *traits index*, we included mass of the male, mass of the female, length, and lifespan of the species. We obtained the data from the same resources as mentioned in the *traits index*. We used continuous variables where possible. We also included the global tolerance of species to climatic conditions in their breeding range; we included the mean, median, maximum, and minimum of the annual mean temperature, the maximum temperature of the warmest month of the year, the mean temperature of the warmest quarter of the year, and the annual precipitation (e.g., the mean for the global breeding range of a species is the annual mean temperature that is given for each square kilometer in its breeding range). Global breeding ranges of the species were obtained through BirdLife International and NatureServe (2013). Information for the Arctic Redpoll (*Acanthis hornemanni*) was lacking, and the species was therefore excluded from this part of the analyses. Current climatic variables were obtained from WorldClim (available online). A large number of these climatic variables were strongly correlated ($r \geq 0.60$, Graham 2003). We only included those climatic variables that were most relevant according to random forest analyses and did not strongly correlate with each other. Finally, variables were omitted stepwise from the random forest until the best model was left. We used the Cohen’s Kappa statistic to test for significance. All statistical analyses were conducted in R version 3.1.1 (R Core Team 2014).

**Results**

We found that 15% of the bird species included in this study are predicted to experience a reduction in their breeding range, according to the species distribution models based mostly on climatic variables (Appendix S1: Table S1). Two of these were predicted to lose their entire breeding range in the study region: the Siberian Jay (*Perisoreus infaustus* [see Appendix S1: Figs. S1 and S2]), currently able to breed in approximately 19% of the study region according to the models, and the Red-flanked Bluetail (*Tarsiger cyanurus*) that is currently able to breed in 17% of the study region. The potential

---

21  [http://worldclim.org/current](http://worldclim.org/current)
geographic breeding range of the Siberian Jay was mostly determined by the maximum temperature of the warmest month; the area was deemed suitable for breeding when the maximum temperature of the warmest month was between 15° and 19°C. The potential distribution of the Red-flanked Bluetail, on the other hand, was mostly determined by the annual range in temperature; the area was deemed suitable for breeding when this was between 9° and 10°C.

Another nine species were predicted to lose >90% of their current breeding range in the study region, which were, in order of the largest loss (proportionally); the Horned Lark, Willow Grouse (*Lagopus lagopus*), Rustic Bunting (*Emberiza rustica*), Western Capercaillie (*Tetrao urogallus*), Ring Ouzel (*Turdus torquatus*), Snow Bunting (*Plectrophenax nivalis*), Long-tailed Skua (*Stercorarius longicaudus*), Bohemian Waxwing (*Bombycilla garrulus* [see Appendix S1: Figs. S1 and S2]), and the Siberian Tit (*Parus cinctus*). On the other side of the spectrum were species like the Rook (*Corvus frugilegus* [see Appendix S1: Figs. S1 and S2]), Marsh Warbler (*Acrocephalus palustris*), European Kingfisher (*Alcedo atthis*), and the Eurasian River Warbler (*Locustella fluviatilis*), which currently rarely breed or have relatively small breeding ranges in the study region but are predicted to be able to breed in larger parts of the study region in future. There was a significant negative correlation between the current size and the predicted future size of species’ breeding ranges in the study region, meaning a significant change in the breeding bird community in that the species that are currently widespread breeders will become localized and vice versa (Fig. 2, Pearson correlation, \( r_{179} = 0.250, P < 0.001 \)). This pattern was mainly driven by species that currently only occur in a small proportion of the region, but were predicted to be able to occupy 15–50% of the region in the future (Fig. 2).

Species predicted to be most vulnerable in future are those that scored high on both the exposure index and on the traits index (category “most vulnerable,” Fig. 3). These are, among others, the Long-tailed Skua, the Common Scoter (*Melanitta nigra*), and the Ring Ouzel. Even more vulnerable are those that were classified in this category and already listed on the IUCN Red List of Threatened Species (the Great Snipe) or on a global red list, like the Rough-legged Buzzard, the Red-throated Pipit, the Common Swift, the Horned Lark, and the Bar-tailed Godwit. Also, species like the Rustic Bunting, the Willow Grouse, and the Western Capercaillie, which were predicted to lose over 90% of their current breeding range, were medium vulnerable (category “climate-vulnerable” in Fig. 3), but because of their natural history traits; these species might be more resilient to climate change than the species mentioned earlier. There were also a number of species that scored relatively high (>0.5) on the traits index but relatively low (<0.5) on the exposure index, and thus fall in the category “trait-vulnerable.” These were, among others, the Osprey (*Pandion haliaetus*), the Caspian Tern (*Hydroprogne*

![Fig. 2](image-url)  
Fig. 2. Correlation (solid line) between the current size and the predicted future size of bird species’ breeding ranges, shown as percentage of the total available, which equates to the entire study region. Range sizes were based on the average of the 10 replicates as generated by species distribution models (SDMs). Species above the dashed line are predicted to have smaller future breeding ranges whereas those below the dashed line are predicted to have larger future breeding ranges.

![Fig. 3](image-url)  
Fig. 3. Representation of the bird species in the vulnerability matrix with the trait index on the \(y\)-axis and the exposure index on the \(x\)-axis.
VULNERABILITY OF BIRDS

January 2017 227

VULNERABILITY OF BIRDS

The Spotted Redshank (*Tringa erythropus*), the Red-necked Phalarope (*Phalaropus lobatus*), and the Greater Scaup (*Aythya marila*). A number of traits some of these species have, like ground nesting, habitat specialism, long-distance migration, low average clutch size, and low number of broods, might make them vulnerable to climate change, even though their potential breeding range might increase based on direct climatic impacts alone. Species that received a low score on both indices (category “least vulnerable,” Fig. 3) are thought to be least vulnerable based on our matrix. These were, among others, the House Sparrow (*Passer domesticus*), the Chaffinch (*Fringilla coelebs*), the White Wagtail (*Motacilla alba*), the Willow Tit (*Parus montanus*), and the Three-toed Woodpecker (*Picoides tridactylus*).

Fig. 4 shows the number of species that are listed on the Swedish red list for threatened species (see footnote 6) per vulnerability class as assessed by our analyses. Species classified as most vulnerable by our matrix also had the highest percentage of species already listed as vulnerable (25%) or endangered (13%; Fig. 4) within that category. Species classified as least vulnerable by our matrix had the highest percentage of species listed as least concern (78%; Fig. 4).

The random forest analyses showed that the global tolerance of species to climatic variables was important in determining whether the species studied are predicted to experience future contraction or expansion of their breeding range in the study region. The median of the maximum temperatures of the warmest month per grid-cell and the minimum of the annual mean temperatures per grid-cell of the global breeding ranges were among the most important in predicting the fate of species’ breeding ranges in the study region (Figs. 5 and 6). Among the natural history traits, the number of incubation days (with species incubating for longer periods being more vulnerable) and whether or not a species is a habitat specialist (with those birds with specific breeding habitat requirements, such as needing large amounts of dead wood, being the more affected ones)
were the most important in predicting whether species’ breeding ranges increase or decrease in future (Fig. 6). The size of the future breeding range compared to the current was significantly correlated with the median of the maximum temperatures of the warmest month (Pearson correlation, $r_{179} = 0.400$, $P < 0.001$) and the minimum of the annual mean temperatures (Pearson correlation, $r_{179} = 0.250$, $P < 0.001$), but not with the number of incubation days (Pearson correlation, $r_{180} = -0.020$, $P = 0.770$). There was also no significant difference between the size of the future breeding range compared to the current and whether species were habitat specialists.
or not (Welch’s unequal variances \( t \) test, \( t_{98} = -1.671, P = 0.098 \)). However, breeding habitat specialists were significantly over-represented among species that were predicted to lose part of their breeding range in future due to climate change (Pearson’s chi-square, \( \chi^2 = 15.686, df = 1, P < 0.001 \)). The 20% of the species that were set aside to test the accuracy of the prediction of the random forest were predicted significantly better than random (Cohen’s \( \kappa = 0.485, z = 3.300, P < 0.001 \)).

**Discussion**

Our results show that although the majority of birds currently breeding in or just south of the European Subarctic and Arctic region may be able to increase their breeding range in future, the number of bird species that are likely to lose part of their breeding range in the region is still considerable (15% of the bird species studied). These species were generally associated with climates that remain cool throughout the breeding season (i.e., low maximum temperatures of the warmest month and low annual mean temperatures). These climatic conditions are, however, predicted to (partly) disappear in the near future. In addition, many of these species were habitat specialists, meaning that they breed in habitats with specific conditions that warrant their breeding success, such as rocky shores and mires. The vulnerability matrix for Subarctic and Arctic breeding birds, which is based upon their direct and indirect vulnerability to future climate change, may help identify which species are likely to need additional conservation efforts in future, something SDM-based assessments on their own could do to a lesser extent.

A species like the Caspian Tern is predicted to increase its breeding range in future due to climate change. However, it is regionally listed as vulnerable (see footnote 6) and it received a high vulnerability index because of its natural-history traits; for instance, the fact that the species is a long-distance migrant (>6,000 km [Shiomori et al. 2015]) likely increases its vulnerability. The loss of a climatic niche is a threat to all species, but migratory species are likely to rely on different climatic niches during their breeding season than at their migration and wintering grounds (Elphick 2007). Moreover, suitable stopover sites are also highly important for accumulation of energy for their journey (Elphick 2007). Although species like the Caspian tern may increase their breeding range, for a migratory species, problems at stopover sites or at wintering grounds may be sufficient for large population declines (Baker et al. 2004, Iwamura et al. 2013).

Climate change may also have other adverse impacts on migratory species. The Arctic environment is characterized by extreme seasonality and migratory species have adapted to exploit the short but productive summer season (Carey 2009, Gilg et al. 2012). However, climate change is altering the snow melt regime and subsequent vegetation growth and invertebrate emergence, which may amplify temporal mismatches between timing of migration and peak food availability, or between avian predators and their prey (Both et al. 2006, Möller et al. 2008, Gilg et al. 2012). Mismatches may be especially pronounced in highly seasonal environments, like those at high latitudes, and can have large consequences for the reproductive success of migrating species (Post and Forchhammer 2008). It is thus not surprising that many migratory birds show population declines (Rappole and McDonald 1994, Donaldson et al. 2000, Both et al. 2006) and rank among the most endangered species.

Furthermore, the Caspian Tern depends on a specific biome (coastal) during the breeding season, which does not increase its chances of persistence either. Shorebirds and coastal birds may face an increasing threat. First, the ecosystems they rely on face threats due to likely increased shore erosion (Brown and McLachlan 2002). Shorebirds will also face habitat loss caused by inundation as a result of sea-level rise (Shuford and Craig 2002, Iwamura et al. 2013). Second, shorebirds are predicted to be affected by the negative impacts of increases in near-shore sedimentation, caused by ongoing ice-melt, on marine invertebrates that are key to their breeding success (Barnes and Kaiser 2007). Third, shorebirds are likely to be threatened by newly established predators like the American mink (Nordström et al. 2003), that are likely to be able to benefit from climate change in future (Hof et al. 2012b), especially in combination with ground nesting strategies. The regional extinction of the Atlantic puffin (Fratercula arctica) in Sweden was, for instance, partly caused by the American mink (Tjernberg 2010b). Introduced West-European hedgehogs have also had devastating effects on shorebird populations by predating on eggs (Jackson et al. 2004). A large number of species, both potential mammalian and avian predators and competitors, may become widespread in Subarctic and Arctic Europe in future, as shown by this study and others (Hof et al. 2012b, 2015).

This will likely further increase the pressure upon the species already inhabiting the region, especially those that may suffer directly from climate change. Moreover, a change in the breeding bird community could have cascading effects on other organisms such as insects.

Our matrix also helps in identifying which species may need less conservation attention. However, even though some species are not thought to be particularly vulnerable based on our vulnerability matrix, there are other factors we did not take into account that may make them vulnerable. One is its current status in the study region. The Three-toed Woodpecker is, for instance, currently listed as near threatened on the Swedish Red List. Numbers have been falling dramatically in the last century, largely due to aspects not directly related to climate change and thus not accounted for in our matrix. In the case of the three-toed woodpecker the decline is thought to be due to habitat loss caused by intensive forestry practices (Tjernberg 2010a).

The results of our study are sensitive to both the quality of the underlying data and to the choices made in the analyses. For example, inclusion of more traits might have improved the trait vulnerability index and ability to predict future population trends. One such trait is
fledgling survival or reproductive success. This trait was the most important in predicting the conservation status of marine mammals (Davidson et al. 2012). Reproductive success of bird species can vary widely which has direct consequences for species’ vulnerability and resilience to changes. We were unable to include it in our matrix since we lacked data for over 50% of the species studied. Similar to mammals, bird species with a particularly low production of offspring may be more vulnerable than our current predictions based on the vulnerability matrix suggest. The lack of such basic natural history data, despite that birds are one of the most studied organisms, is potentially dire in the face of an imminent change in bird community composition due to climate change.

Although the choice of thresholds and how to weigh the relative importance of traits remain important challenges, our approach should be robust to our main aim, i.e., identifying those species in the regional species pool that require extra conservation attention as a result of climate change. We identified a group of species whose climatic niche is expected to decrease, and which have several traits making them vulnerable, making their future in the region uncertain. While some might be able to withstand climate change due to favorable natural history traits, others might not. For example, a species like the Northern Lapwing (Vanellus vanellus) may be able to have a second brood in the region since it has shown to do so in other parts in its breeding range that have a warmer climate with a longer growing season (Baumann 2006). For a species like the Long-tailed Duck (Clangula hyemalis), which is globally assessed as vulnerable (Birdlife International 2012), regionally assessed as endangered (Helcom 2013), predicted to lose part of its breeding range in the study region in future due to climate change, and has several natural history traits that might make it extra vulnerable to climate change, urgent actions are needed. In the case of the Long-tailed Duck, increased monitoring, especially of their breeding grounds, i.e., lakes and mires in the tundra and boreal forests (Ottvall et al. 2008), and alleviating other threats, such as hunting, should be considered. Incorporating species traits into vulnerability assessments may also improve our understanding of how species cope with extreme weather events caused by climate change. For instance, climate change is expected to influence freeze–thaw dynamics of snow during winter, which could influence sedentary species like the rock ptarmigan (Hansen et al. 2013). The increase in freeze–thaw cycles has also been suggested to be related to declines in gray jay at the southern edge of its range in the Canadian boreal forest (Sechley et al. 2015). Weather events like storms or heavy rain may also have severe consequences for seabird colonies, particularly during the nesting period (Gilg et al. 2012). On top of the effects future climate change may have on species, traits like the ones mentioned should be taken into account. For the species found to be both vulnerable and exposed to climate change in our general assessment, additional data based on traits such as fledgling survival, reproductive success, and the conditions during the time needed for molting (Knudsen et al. 2011), and other factors, like anthropogenic pressures and tolerance to climatic extremes (Zimmermann et al. 2009), may be needed to design effective conservation strategies.

Our aim was to gain a general understanding of relative inherent vulnerability of a large number of species in the study region, and our simplistic approach to create the traits index was deemed sufficient to meet the aim of the study. Using a less simplistic approach, such as the one used by Pocock (2011), for all species assessed would currently be logistically infeasible, because the required ecological data (e.g., mass of hatchlings and fledglings) are unfortunately lacking for most species studied. Approaches similar to ours were used by, among others, Amano and Yamaura (2007), Gardali et al. (2012), Foden et al. (2013), and Triviño et al. (2013). Our vulnerability matrix helps predict which species will likely be most in peril in a future warmer climate. According to our analyses, most conservation effort should be placed upon the great snipe, a species classified in the category “most vulnerable” and already listed on the IUCN Red List of Threatened Species and on the Finnish, Norwegian, and Swedish red lists, and on other species classified in this category and already listed on regional lists. Changing tree limits and increased overgrowth of wetlands due to reduced grazing pressure and climate change have been mentioned as possible further threats to the Scandinavian Great Snipe population (Ostnes et al. 2014). Local conservation effort should thus be focused on preserving its breeding and lekking habitat, which, in Scandinavia is concentrated on rich fens, calcium rich wetlands, and along tree limits in mountainous areas (Kålås et al. 1997). The total acreage of rich fens has historically been reduced by human draining activities for agricultural purposes and many of the remaining rich fens are currently threatened by acidification, eutrophication, and overgrowth by trees (Vasander et al. 2003, Evasdotter 2011). The reproductive success and conservation status of the great snipe in Scandinavia fluctuates with predator pressure (i.e., in years with high lemming abundance the predation pressure on great snipe chicks is reduced) and weather conditions (e.g., flooding may damage nests and draughts may affect food availability; UNEP/AEWA Secretariat 2004). The populations of Siberian Jays and Red-flanked Bluetails may also need to be monitored closely since our study suggests that the projected higher summer temperatures and the increase in annual temperature range in our study region have the potential of displacing these two species from their current breeding grounds. In addition, the species falling in the category “most vulnerable,” but not (yet) listed on regional red lists may need to be monitored. Least conservation effort could go to the species falling in the category “least vulnerable” that are not listed on regional or global red lists at present. However, there are other factors, not necessarily related to climate change, that we did not take into account in our matrix. Negative impacts of, for instance,
intensive forestry, agriculture and hunting may severely affect population sizes (Fox and Madsen 1997, Donald et al. 2001, Imbeau et al. 2001). Also, four of the species we assessed are currently already listed on the IUCN Red List of Threatened Species: the already mentioned Great Snipe and Long-tailed Duck, but also the Eurasian Curlew (*Numenius arquata*) and the Velvet Scoter (*Melanitta fusca*; see footnote 8). One species, the Arctic Redpoll, has not yet been assessed for the IUCN Red List. These species should therefore receive attention irrespective of their placement in our matrix.

**Management Implications**

A change in climate may not directly affect all species. It is by studying species’ exposure, sensitivity and adaptive capacity to climate change that we may understand what and where their specific vulnerabilities are. This vulnerability matrix provided additional information over climate-only based models that, by incorporating a traits index, enabled us to identify which climate-vulnerable species were more vulnerable to climate change because of their natural history traits. Furthermore, we identified a number of species that were vulnerable to climate change based on their natural history traits but were not identified as vulnerable based on their exposure to the consequences of climate change to their local environment alone, which highlights the importance of linking exposure and trait based indices. Furthermore, a noteworthy conclusion we drew from compiling the natural history traits index for our vulnerability matrix is that some key natural history traits needed for estimates of bird population status (such as number of fledglings per year) are lacking for most of the birds studied. This is somewhat surprising given the large number of studies on birds breeding in Fennoscandia and the large number of bird enthusiasts in the study region, which is reflected by the large amount of species occurrences in databases like the Global Biodiversity Information Facility. We therefore call for more detailed studies to collect natural history trait data, especially for under-studied species.

Our vulnerability matrix provides a framework that incorporates climate change and natural history traits in the assessment of species vulnerability that will help improve general assessments of sensitivity of assemblages to climate change as well as evaluations of species for red lists. Our results further show that incorporating natural history traits in studies that investigate impacts of future climate change on species may better identify vulnerable species and therefore improve conservation planning when focus and monetary restrictions are necessary. Studies like ours emphasize the need for international collaboration in conservation efforts of threatened species as climate change will likely increase species’ mobility. There is an increasing need for cross-country conservation efforts and enhanced collaboration in order for species’ conservation efforts to be successful. Focusing on natural history traits will provide management agencies with a list of specific actions that could be taken to maintain threatened bird populations (such as providing nesting sites and protecting important breeding areas from forest fragmentation). Conservation strategies can be designed to target these species specifically, which would have to encompass efforts to conserve not only their breeding grounds, but also stopover sites and wintering grounds. Management of invading and newly establishing predators may also be necessary to preserve a number of species, specifically ground nesting ones. Some species may also face increased competition as a result of bird species expanding poleward, calling for actions to minimize impacts, e.g., by restoring breeding habitats that are in short supply as a result of land-use activities. Given the combined effect of climate change and likely changes in land-use and other anthropogenic factors, it will be imperative to adjust conservation strategies to changing climates for the survival of species.

**Acknowledgments**

This project was funded by the Nordic Council of Ministers. We are grateful to BirdLife International and NatureServe for providing global breeding ranges of the species studied and we thank the anonymous reviewers for suggestions that improved this manuscript.

**Literature Cited**


**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1434/full